

山茶科濒危植物猪血木的花器官发生*

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摘要: 利用扫描电镜首次观察了山茶科极濒危植物猪血木 (*Euryodendron excelsum*) 的花器官发生过程。猪血木的花为两性完全花, 萼片和花瓣均为 2/5 螺旋向心发生, 单轮排列, 且有逆时针和顺时针两种方式。雄蕊的形成是先形成一个环形分生组织, 然后在环形分生组织上以 2/5 螺旋产生 5 束雄蕊原基, 每一束雄蕊原基的第一雄蕊原基都是在对萼的位置产生, 其它的雄蕊原基在其两侧产生。3 心皮顺序发生, 愈合成 3 室单子房, 柱头平截不裂。猪血木与山茶亚科的花器官发生明显不同。

关键词: 山茶科; 厚皮香亚科; 猪血木属; 花器官发生

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Early Floral Development of Endangered *Euryodendron excelsum* (Ternstroemiaceae: Theaceae)

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Abstract: The floral development of a critically endangered plant *Euryodendron excelsum* from Ternstroemiaceae (Theaceae) has been observed under scanning electron microscope (SEM) for the first time. The flower of *E. excelsum* is bisexual and teleianthous. Five sepal primordia are initiated 2/5 spirally and arranged in one whorl when mature, and so are petals. Sepals and petals are initiated in the same order either clockwise or counterclockwise in the same flower. The androecial part is a ring primordium in the beginning. The first five stamen primordia are initiated on this ring primordium at antisepalous positions and then other stamen primordia appear on two sides of each of the first five primordia. Finally a total of 2/5 stamen primordia are initiated from the ring primordium and arranged in one whorl but could be grouped into 5 fascicles. Three sequentially initiated carpels compose an ovary which has an axile-central placenta with three locules and a truncate and indehiscent stigma. The floral development of *E. excelsum* is distinctly different from plants in Theaceae.

Key words: Theaceae; Ternstroemiaceae; *Euryodendron*; Floral ontogeny

Euryodendron excelsum is a monotypic generic plant of Ternstroemiaceae, Theaceae. The species is endemic to China, only distributed in Guangdong Province (Lin, 1998). It is a critically endangered species (Hilton-Taylor, 2000), previously only more than 80 living plants found in wild (Wang *et al.* 2002). Morphologically *E. excelsum* is between *Eurya* and *Cley-*

era. Its phylliform and phyllotaxy are similar to *Eurya*, while its flower structure is similar to *Cleyera* (Chang, 1963). Thus the species is very important for understanding the relationships the genera in Ternstroemiaceae. As it is an endangered species, study on it will also serve for its conservation biology.

Ternstroemiaceae is traditionally a subfamily of

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Theaceae, although it was established as a separate family Ternstroemiaceae in early nineteenth century. The circumscription of family Theaceae has been greatly modified over the past 100 years. Cronquist (1981) included four subfamilies in Theaceae: Theoideae, Ternstroemioidae, Bonnetioidae and Asteropeioidae. Dahlgren (1983) excludes Bonnetioidae, and Airy-Shaw (1936), Hutchinson (1969), Rouleau (1981), Goldberg (1986), Thorne (1992) and Takhtajan (1997) only recognize Theoideae (or Camellioideae) and Ternstroemioidae. So most modern plant systems accept Theoideae (or Camellioideae) and Ternstroemioidae as core groups of Theaceae.

Recent molecular studies, nevertheless, provided new evidences and indicated different phylogenetic relationships in Theaceae. Most studies found Theoideae and Ternstroemioidae to each be monophyletic but not sister to each other (Morton *et al.*, 1996, 1997 a, b; APG, 1998; Savolainen *et al.* 2000; Soltis *et al.* 2000; Anderberg *et al.* 2002), and APG (1998) further suggested two distinct families Theaceae and Ternstroemiaceae. But in later studies using more samples the monophyly of Ternstroemioidae was only moderately supported (Prince and Parks, 2001) or not supported by mitochondrial *matR* sequences (Yang *et al.* 2006). Therefore the recognition of two distinct families should be accepted with caution, and the relationships between Theoideae and Ternstroemioidae still need further studies. For various reasons, Theoideae received more attention while Ternstroemioidae was studied much less from all respects. Few studies from Ternstroemioidae make it difficult to analyze the evolutionary relationships in Theaceae, so the study on taxa of Ternstroemioidae is urgently in need.

In the last decades, floral development has come to be indispensable for an integrated study of any higher rank taxon (Endress, 1994; Tucker, 1996). In Theaceae, studies on floral ontogeny of most genera in Theoideae were studied by different authors (Erber, 1986; Sugiyama, 1991; Tsou, 1998), but there has been no report on Ternstroemioidae. The objective of this study is to investigate the floral ontogeny of *E. excelsum*, therefore to provide evidence for systematic relationships of *Euryodendron* with other taxa and for further study of Ternstroemioidae.

Materials and Methods

Plant materials of *E. excelsum* were collected in June 1998 from Bajia, Yangchun County, Guangdong Province. Flowers of all stages were fixed in formalin-acetic acid-alcohol (FAA, formalin acetic acid 70% ethanol = 1 : 1 : 18). Voucher specimens (He Han & Wang Yue-Hua, 998001) were deposited at the Herbarium of Yunnan University. Materials were generally examined and carefully dissected under a dissecting microscope in 95% ethanol, and dehydrated through an ethanol-isoamyl acetate series, and dried with a Hitachi HCP-2 critical point dryer. Samples were then mounted on stubs and Au Pt sputter coated with SPI-Module Sputter Coater. Prepared samples were examined with Hitachi S-800 Scanning Electron Microscope (SEM) and recorded on Shanghai Panchromatic film.

Results

Initiation of floral primordium and bract

Every year new leaves sprout from late March to early April, although *E. excelsum* is an evergreen tree. Floral buds are subtended by small vegetative leaves on new branches or by bud scales on perennial branches. The floral primordia are hemispherical in shape (Plate 1). With the development of floral primordia, the first bractlet primordium (Plate 2) gradually differentiates from the side of the apex. Then another appears in the opposite position and is covered by the first one. The two bracts are same sized in mature flowers. Filiform hair gradually appears with the development of bracts, so the bracts are finally hairy (Plate 3).

Perianthial initiation

There are 5 sepals and 5 petals in *E. excelsum*, but in the beginning the 10 perianth primordia are homogeneous in appearance and they differentiate into sepals or petals only at late floral development. The perianth primordia are initiated quincuncially and their bases are basically triangular. The sequence of initiation of the sepals and petals is spiral throughout, following a 2/5 phyllotactic pattern either clockwise (Plate 3, 5, 6) or counterclockwise (Plate 4), but in same sequence in one flower. Each primordium is round-domed in the beginning. With the continual activity of the meristem, these primordia elongate and heighten gradually with more expansion in lateral directions. During this progress, the primordia differentiated: the first initiated five developed into small, stout, and brownish sepals; the latter five became large, flattened, and white-yellowish petals. The calyx and corolla are distinct, and the five sepals are arranged in one whorl, as are the five petals (Plate 6, Plate

: 16), although the members of each whorl is via spiral initiation. So the basis of each whorl is quin-quangular (Plate : 16) in fully developed flowers.

Androecium initiation

After the fifth petal is initiated, the floral apex looks like a flattened pentagon (Plate : 7), then becomes saucer-like when the androecium is about to originate (Plate : 8). When the gynoecial part begins to appear, the androecial part is a ring-like primordium. The initiation of stamen primordia is not simultaneously evenly sized. The first five stamen primordia are initiated antiseptally in a 2/5 spiral on the ring-like primordium (Plate : 10 - 15), and the spiral direction is same as that of the sepals. Then the other stamen primordia appear at two sides of each primordium. And again the other primordia are initiated at two sides of these previous three primordia, so that a total of four stamen primordia appear around each of first five primordia and finally a total of 25 stamen primordia exist in every flower. During the process of androecium initiation, as the previously initiated primordia are bigger than the later ones (Plate : 12, 13, 15), every five primordia make up a fascicle, with the first one as the center (Plate : 12). With the development of the later primordia, the size differences among the primordia become smaller and smaller and finally all stamens are same in size and arranged in one whorl (Plate : 13).

All stamen primordia are hemispherical at beginning, then turn ellipsoidal before eventually become column-like in shape (Plate : 15 - 18) and they are same sized as the differentiation of sepals and petals finished. Shortly, with the middle of the stamen primordia broadening, the primordia begin to differentiate (Plate : 19), from which the upper triangular part will become anther and the lower columnar part will become filament (Plate : 20). The edges of mature anther will be covered with hairs (Plate : 20). Finally, a total of 20 - 25 stamens, with the length of 1.5 - 2.0 mm, are arranged in one whorl.

Gynoecium initiation

The gynoecium of *E. excelsum* comprises three carpels (Plate : 9, 10, 11, 12, 13, 16), but occasionally two-carpellate gynoecia (Plate : 14, 15) could be seen. The carpels are initiated separately (Plate : 9, 10, 11), within the above-described central flattened base of the floral apex before stamen

primordia emerge. Carpel primordia appear as hemispherical bulges in the beginning, and then expand more in lateral directions. Later, the two lateral sides of such a primordium involute and so that make the carpellary chamber becomes more and more evident on the ventral side. When stamen primordia become finger-shaped, the fusion of carpels is basically complete (Plate : 17, 18), and the gynoecium looks like a ball. Then, with the differentiation of stamen primordia and the development of anthers, a single and unbranched stigma (Plate : 19) emerges and the gynoecium become bottle-shaped. The fully developed flowers all possess axile-central placentas with two or three locules, and the ovary is evidently superior, with the attachments of both androecium and gynoecium on the flat surface of the receptacle. The development of a two carpellary gynoecium is similar to a three carpellary one (Plate : 14, 15).

Discussion

Ternstroemiaceae includes about 10 genera and 6 occur in China. No comparable work has been done to other taxon in Ternstroemiaceae, but majorities of Theaceae, seven from total ten genera, were studied by different authors (Erber, 1986; Sugiyama, 1991; Tsou, 1997, 1998). According to Tsou (1998), early floral development in Theaceae shows diversity in several aspects and could be grouped into two groups according to these differences: in some taxa the perianth primordia only differentiate into sepals and petals at late development and this is called group I, while in group II the calyx and corolla are distinct at inception. Moreover, group II can be divided into two subgroups, in group IIa individual stamens are initiated from five fascicle primordia and the placentation is axile-basal, whereas in Group IIb, no androecial fascicles are formed and the placentation is axile-central. In each group the floral development is very similar and the difference in each group is minor. Tsou (1998) concluded that the two groups represent two evolutionary lineages. Group I is the earlier evolved lineage and Group II is the later derived lineage. However, the differences of floral development only exist in the early stage of development. With the development goes on, the differences become small and the mature flowers in Theaceae are all similar in appearance: they all have sepals and petals, and they all have numerous sta-

mens .

Compared with Theoideae, the floral organogenesis of *Euryodendron excelsum* has some distinct features: it has only one whorl of stamens and the initiation pattern of stamen primordia is rather special .That there is only one whorl of stamens in *E. excelsum* is not newly found in this study, as it can be seen by naked eyes, and this has traditionally been one of the differences between Theoideae and Ternstroemioideae (Cronquist, 1981; Dahlgren, 1983; Hutchinson, 1969; Thorne, 1992; Takhtajan, 1997) . This distinction may be considered only numerical and insignificant if not this study .This study has indicated that this is not only numerical but also substantial . In *E. excelsum*, when the androecial part is about to originate, it is a ring primordium .Then five stamen primordia appear at antisepalous positions, that is, alternate with petals . Following that, a total of four stamen primordia are initiated on two sides of each of these first five stamens in a laterally centrifugal sequence, and thus every five primordia, the very first one and the later four, form a fascicle .In Theoideae, the ring primordia at the beginning of androecium initiation only occur in group I but the following development is not like that of *E. excelsum* .In this group, from the ring primordium, about 10 - 13 stamen primordia appear along the footline to form the first whorl, and then the second and the following whorls are initiated in a centrifugal sequence (Tsou, 1998) .During this process, stamen primordia of each whorl are not initiated synchronously, but they are definitely not initiated in the special sequence as that of *E. excelsum* . In group IIa and group IIb of Theoideae, no ring primordium but five fascicle primordia or androecial zone appear before stamen primordia

initiation (Tsou, 1998) . The fascicle primordium in group IIa is a bulge in form and a pro-primordia structure, and the stamen primordia on each fascicle are initiated nearly simultaneously (Tsou, 1998) . So the fascicle primordia in this group, though used same word“ fascicle ”, is a structure before individual stamen appear and different from the concept of our current study .In group IIb of Theoideae, stamen primordia are initiated from five androecial zones (Tsou, 1998) . Five stamen primordia appear first on the lowermost margin of each zone, and each initiation zone expands upward and outward continuously, followed immediately by the inception of the stamens of higher orders (Tsou, 1998) . Thus the primordia initiation in group IIb is also different from that of *E. excelsum* . The floral developmental characters of Theoideae and *Euryodendron* are summarized in table 1 .

As the only representative of Ternstroemioideae, *E. excelsum* in this study shows very different early floral development . It is hard to conjure this floral development type has some connection with or has derived from any type of Theoideae . So from the present study, we could conclude that *E. excelsum* is not closely related with Theoideae . Therefore this result also support that Ternstroemioideae is only distantly related with Theoideae . Though using one genus to represent Ternstroemioideae seems not solid, this result has been supported by other studies . Embryological studies on members of Ternstroemioideae, e.g . Yang and Min s (1995a) work on *Pyrenaria* and *Tutcheria* and Tsou s (1995) study on *Adinandra*, *Cleyera* and *Eurya* also indicated that the embryological characters of Ternstroemioideae are very different from those of Theoideae, suggesting they are two distinct groups .

Table 1 Comparison of the floral development of Theoideae and *Euryodendron*

Taxa	Perianth	Androecium	Gynoecium
Theoideae group	11-16 perianth primordia initiated in a spiral sequence . The young perianth members are homogeneous at inception, only differentiated in later stage .	Numerous stamens initiated individually and centrifugally on the whole androecial region . Stamens numerous, 2-5 whorled .	2, 3 or 5 carples, axile-central placenta
Theoideae group a	Sepal primordia and petal primordia are distinct at inception . The five sepals and the five petals are arranged in two whorls .	Individual stamen primordia initiated from five fascicle primordia centrifugally . Stamens numerous, > 5 whorled .	5 carples, axile-basal placenta
Theoideae group b		Individual stamen primordia initiated from five peripheralslopes centrifugally . Stamens numerous, 2-3 whorled .	3 or 5 carples, axile-central placenta
<i>Euryodendron</i>		Individual stamen primordia initiated from ring-like primordia . Every five primordia form a fascicle . Stamens 25, 1 whorled .	2 or 3 carples, axile-central placenta

Some other studies also have been conducted on members of Theoiidae and Ternstroemiaceae. The flowers of Ternstroemioidae members are less diverse than Theoiidae members. Studies on pollen morphology (Dickison, 1982; Wei, 1997; Xu *et al.* 2005) and work on Leaf epidermis (Zhang and Zhuang, 2004) all indicated that members of Theoiidae have greater diversity than members of Ternstroemiaceae in these respects. Molecular works, on the contrary, have proved the monophyly of Theoiidae while monophyly of Ternstroemiaceae was not supported (Yang *et al.* 2006). In Prince and Parks (2001) phylogenetic study on Theaceae s.l., 7 species from 5 genera of Ternstroemioidae were sampled, but *E. excelsum* was not included. In their study, Theoiidae (Theaceae s.s.) as a monophyletic group was strongly supported while Ternstroemioidae was only moderately supported, and this two clades were not sister to each other. Yang *et al.* (2006) conducted another phylogenetic study on Theaceae using mtDNA *matR* sequence and 6 species representing 6 genera in Ternstroemioidae were sampled, in which *E. excelsum* was included. But in their study, 6 taxa from Ternstroemioidae did not even form one clade while Theoiidae was strongly supported as a monophyletic group. This has led us to reconsider the relationships among taxa of subfamily Ternstroemioidae.

The present study provided new evidence of discrepancies between Ternstroemioidae and Theoiidae. However, as we have addressed above, the relationship of them is complicated. Further studies on more members are urgently needed to clarify the relationships among groups in Ternstroemioidae.

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Explanations of Plates

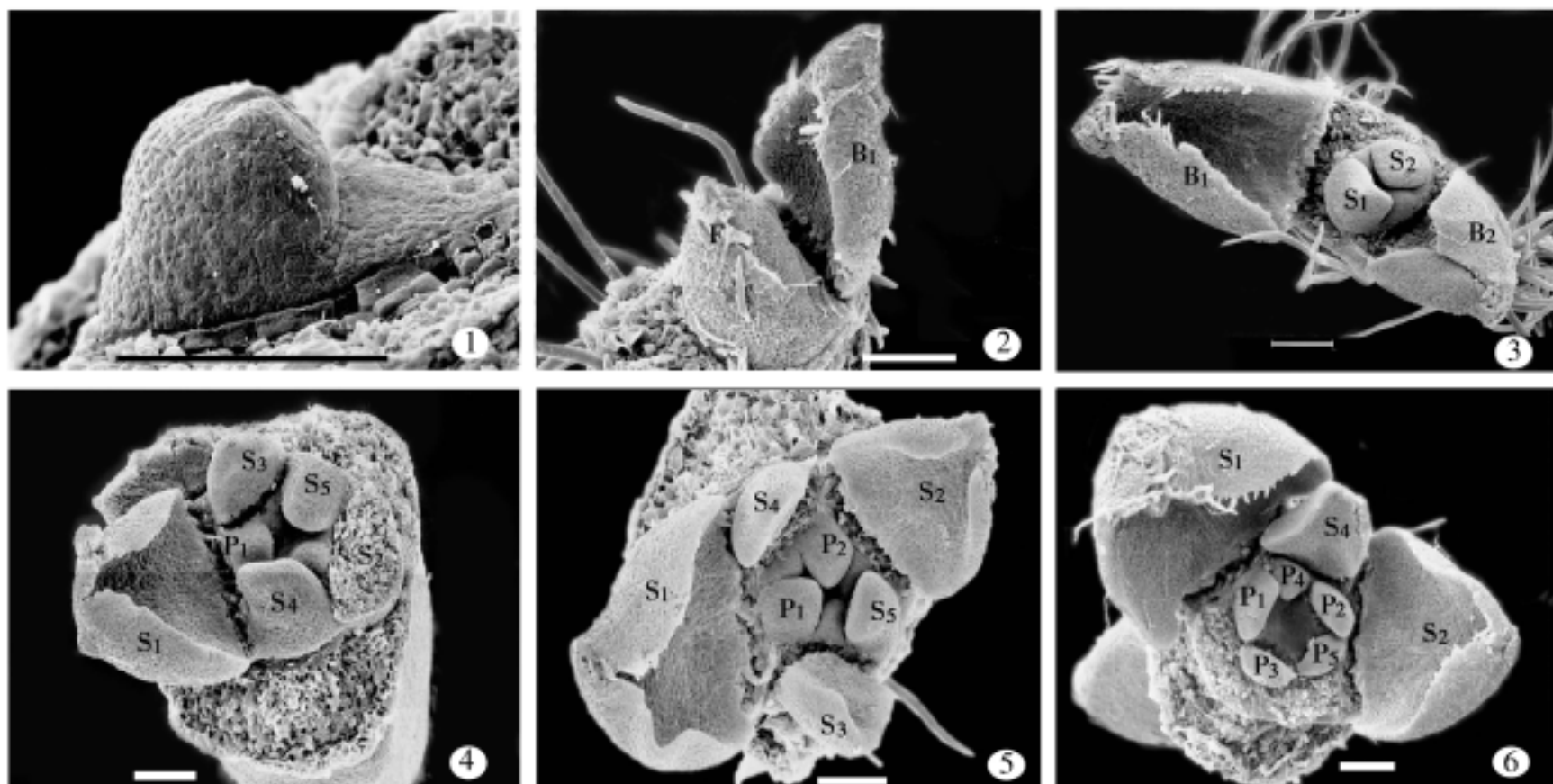
Plate : 1-6 . Floral development of *E. excelsum* . 1 . the hemispheri-

cal floral primodium has grown away from the bud scales; 2 . The floral meristem has bifurcated, leaving a lateral branch complex meristem adjacent to the first bract (B1) and the floral meristem (F) adjacent to the second bract; 3 . The initiation of two bracts with some long hair, and successive initiation of the first three sepal primordia in a clockwise order at the apex of the flower; 4 . Top view of the bud, showing the five sepals and first two petals initiated in a counterclockwise order; 5-6 . Top views of the young flower, showing initiation and the shape of sepals and two petals primordia in a clockwise order, please note that sepals and petals are initiated in the same order in the same flower .

Plate : 7-20 . Floral development of *E. excelsum* . 7 . Top view of the floral apex from 6, two sepals are removed and the other three existed . Showing the apex is pentagonal and flat; 8 . Top view of the floral apex after 7, showing the concave floral apex; 9 . Floral apex showing initiation of the three carpel primordia, in different sizes, and the ring-like androecial primordium around the carpels; 10-11 . Top view of the floral apex, three carpels just slightly fused at the base, and the earliest stamens just initiated on the ring-like androecial primordia; 12 . Lateral view of 13, some stamens appear clearer and their development is not synchronous; 13 . Top view of 12, three carpels fused deeply, five stamens are clearly bigger than others; 14 . Two carpels are initiated in different sizes, and some of the earliest stamens are just initiated; 15 . Two carpels fused after 14, and five stamens are bigger than others as in 12 and 13; 16 . Floral bud with sepals and petals removed, showing five sepals and five petals arranged in two whorls although they are initiated in a spiral, and both have a quinquangular base; 17-18 . With the development of the floral bud, all stamens reach the same size; 19 . Three carpels fuse completely and form a truncate style; partial stamens begin to differentiate; 20 . All stamens differentiated into anther and filament gradually, and some long hair grows on the stamens with the development of the flower .

张瑞菊等：图版

ZHANG Rui-Ju *et al.*: Plate



张瑞菊等：图版

ZHANG Rui-Ju *et al*: Plate

